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STUDIES OF THE MECHANISM OF THE PHYSIOLOGICAL EFFECTS OF CERTAIN MINERAL SALTS IN ALTERING THE RATIO OF TOP GROWTH TO ROOT GROWTH IN SEED PLANTS

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INTRODUCTION

Very few researches are recorded in the field of plant physiology which deal specifically with top-root growth ratios in plants and with the factors that may alter such ratios. In attacking this problem, great difficulties are unavoidably encountered because of the complexity of the medium in which experiments with roots must always be carried on. From the standpoint of physical chemistry, our knowledge as to reactions between plant roots and the mineral nutrient solutions in which they may be growing is not much more perfect than that of reactions among plant roots, soil particles, and soil solution.

The scientific plant grower as well as the physiologist would be greatly aided in their respective fields if there could be furnished a more exact knowledge of the interrelations between the aërial and the subterranean plant parts: as to how intimately interdependent these members are, and also to what extent and under what conditions either may behave independently of the other.

Getting results of physiological value in respect to this problem from investigations with woody plants is a slow and tedious undertaking, yet the field of horticulture and pomology through its numerous experiments in pruning and grafting contains much valuable material which clearly indicates the varying relationships of tops and roots under varying conditions of nutrition and treatment, as well as the necessity of more exact physiological investigations seeking to get at the causes. The fertilizer problem will not be solved either from a scientific or from a practical point of view until more definite information is obtained as to how the particular fertilizer used affects the plant roots, or as to how to localize the effect of a particular treatment in the desired organ.

The investigations discussed in this paper are concerned chiefly with the effects of nitrate ions upon the relative behavior of tops and roots in

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certain plants. There has long been a well defined impression that nitrates check the growth of roots; whether this supposed checking is the result of the action of the salt ions directly upon the roots, or whether the effect is brought about indirectly because of a much more stimulating effect of the salt ions upon the aërial portions of the plant, has been left, in a large measure, unanswered.

STATUS OF THE PROBLEM AS PRESENTED IN THE LITERATURE

Moeller (19) was one of the first workers to call attention to the difference in ratio between tops and roots of plants as they grew in solutions of different concentrations. The more dilute solutions which he used were such that they brought about, as he states, dwarfing of the plants growing in them. It would seem, therefore, that his results should be attributed more to starvation effects than to any definite consequence of the concentration as such. He found that weight of tops was five times that of roots in the normal plants, while in the dwarf cultures the top weight was only twice that of roots. The root systems of the dwarf plants, however, were absolutely smaller than those of the normal.

In 1906, Livingston (17) worked upon the relation between roots and tops in wheat. He grew his cultures in soil, using a "poor" soil from Takoma Park, Md., as the basis. In some of his experiments he used the "poor" soil untreated, in others he added stable manure ranging from 5,000 p.p.m. to 50,000 p.p.m.[1] He drew the conclusion from his work that variation in tops is correlated with the number and length of lateral roots. He found that poor soil inhibits growth of lateral roots and also brings on a premature aging of the cortical cells, both of which conditions inhibit the intake of water. He thus explains the dwarfing of tops in his "poor"-soil plants largely on the basis of an inadequacy of water. Soil cultures are not wholly comparable to water cultures, yet the poverty of certain mineral nutrients in water cultures will bring about a lowered ratio of tops to roots, as Livingston found in his "poor"-soil experiments, and in such case there is no evidence that a deficiency of water supply is a factor. In a soil devoid of nutrients, there would be, undoubtedly, retardation of the growth of both tops and roots.

Harris (12), working in 1913 at Cornell University, sought to determine to what extent the ratio of tops to roots in certain plants is affected by moisture, plant food, and age. He grew plants in aqueous extracts of soil and in sand in which moisture and fertilizer were controlled. His results indicate that all three factors considered in the experiment influence the ratio of tops to roots in a positive way. His experiments with plants grown in solution and in soil, while in no way conclusive as to the relative parts played by moisture and fertilizer in altering ratios of tops to roots, are very suggestive. A brief table (table 1) of some of his results will bring out very well the conclusions.

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[1] P.p.m. = parts per million.

TABLE 1

Fertilizer Treatment	Moisture in Soil	Ratio of Tops to Roots at Maturity (Wheat)
None	30%	8.1 : 1
None	15%	3.1 : 1
Complete	30%	8.7 : 1
Complete	15%	4.1 : 1
Complete with high nitrogen	30%	9.8 : 1
Complete with high nitrogen	15%	2.9 : 1

It will be seen from table 1 that fertilizer and moisture appear to increase the ratio of tops to roots, but that the fertilizer factor plays apparently a small rôle in comparison with moisture.

More or less recently three workers, Tottingham (31), Brenchley (2), and Stiles (29), employing nutrient solutions, have given considerable attention to the relative behavior of tops and roots of plants growing in solutions. But such attention as was given was only a side issue and not the primary aim of their investigations. Because of certain points of similarity running through the works of these three authors, it seems advisable to discuss them together. Both Stiles and Miss Brenchley sought to determine the effect upon growth of certain plants by varying the concentration of the nutrient solution. They disagree sharply as to the range of concentration of nutrients in a solution which will offer favorable growth for plants, yet their results agree fairly well in respect to what they interpret as the effect of concentration on the ratio of tops to roots, and the fact has been pointed out more than once in their works that as the solution decreases in concentration, the ratio of dry weight of tops to roots also decreases. Table 2, taken from their results, brings out these findings.

TABLE 2

Concentration	Full Strength	1/5	1/10	1/20	Duration	Treatment
Stiles						
Series 1, $\frac{\text{Tops}}{\text{Roots}}$	4.0	3.7	3.4	3.0	39 days	Changed often
" 2, $\frac{\text{Tops}}{\text{Roots}}$	3.0	3.1	3.3	2.5	41 days	Changed twice
" 3, $\frac{\text{Tops}}{\text{Roots}}$	2.7	3.2	3.1	2.2	42 days	Changed once
Brenchley						
Series 1, $\frac{\text{Tops}}{\text{Roots}}$	2.7	2.5	2.4	2.5	49 days	Changed often
	3.7	2.7	1.8	1.5		Changed once
	2.6	2.2	1.8	1.2		Changed never
" 2, $\frac{\text{Tops}}{\text{Roots}}$	3.3	3.0	2.3	1.9	49 days	Changed often
	2.8	2.3	1.8	1.4		Changed once
	2.6	1.8	1.3	1.0		Changed never
" 3, $\frac{\text{Tops}}{\text{Roots}}$	3.9	3.1	2.8	2.4	49 days	Changed often
	2.3	2.3	1.9	1.6		Changed once
	1.9	1.3	1.2	1.0		Changed never

The full-strength solution employed by Stiles had a total salt concentration of 1,830 p.p.m., while that used by Miss Brenchley contained 3,040 p.p.m. In their investigations both workers grew plants in the full-strength solution and in three dilutions of the same (1/5, 1/10, and 1/20 of the full strength).

In making a critical examination of the results given in table 2 in connection with the dilutions employed, as well as in the light of the possible behavior of salts in very dilute solutions, the question arises as to whether these results are really significant in relation to a varying concentration as such, or whether or not they may be indications of a deficiency of one or more ions. In order that experiments may be conclusive on this point, ample precautions should be taken that the minimum requirements of essential salts are at hand throughout the duration of the experiment, otherwise we may have the lack of some salt as the limiting factor. Certain results to be reported later in this paper show that increasing the concentration alone in a solution, there being adequate nutrients present otherwise, will not give higher ratios of tops to roots than result in another solution with even lower concentration of total salts but of different chemical composition.

As further evidence that concentration in itself is not a controlling factor, table 3, computed from table 15, page 187, of Tottingham's work (31), will be of interest. While the original paper in question does not give the ratios, it does give dry weights of tops and of roots from which the ratios have been calculated. It should be added that these results of Tottingham's are based mostly upon single cultures, and this fact should be considered in evaluating the data.

TABLE 3

	Total Concentration of Salts in Solution (%)							
	.05	.10	.15	.20	.25	.30	.35	.40
Ratio, $\frac{\text{Tops}}{\text{Roots}}$	3.22	3.13	3.17	2.58	3.17	3.03	3.5	3.11

	Total Concentration of Salts in Solution (%)							
	.45	.50	.55	.60	.65	.70	.75	.80
$\frac{\text{Tops}}{\text{Roots}}$	2.91	2.84	3.10	3.00	3.00	3.03	2.91	3.10

In the experiment upon which the table is based, the total concentration of the solution (a modified Knop's solution) varies, as will be noticed, from 500 p.p.m. to 8,000 p.p.m., with no influence whatever, as the figures show, upon the ratios of top to root growth of the wheat plants employed. In another phase of his researches, Tottingham held the concentration constant, but varied the salt proportions of his solution chiefly around monobasic potassium phosphate, which constituted from one tenth to seven tenths of the total salt concentration employed. He actually made up his solutions on the basis of osmotic pressure (.6 percent solution corresponding to an osmotic pressure of 2.50 atmospheres), but we may, for convenience, use total concentrations in the discussion, since for these dilute solutions osmotic pressure varies with the concentration.

Tottingham's variations in the proportion of salts gave a total of 84 solutions. In 28 of these, one tenth of the total concentration was due to monobasic potassium phosphate; in 21 solutions, two tenths; in 15, three tenths; in 10, four tenths; in 6, five tenths; in 3, six tenths; in 1, seven tenths. Cultures were grown in each of the solutions. Using the figures on his triangular diagrams, the top-root ratios have been averaged for at least ten cultures from each of those percentages of monobasic potassium phosphate, giving ten or more solutions, while ratios for all the cultures have been averaged for the remaining triangles. The results are again very suggestive (table 3*a*).

TABLE 3*a*

	Partial Concentration of KH_2PO_4 in a .6% Solution						
	.1	.2	.3	.4	.5	.6	.7
$\frac{\text{Tops}}{\text{Roots}}$	3.1	2.84	2.69	2.57	2.77	2.43	2.42

With the exception of one result, the ratios of tops to roots shown in table 3*a* vary inversely with the concentration of monobasic potassium phosphate in the solution. Whatever importance we may attach to this table, it stands out in contrast to table 3 in emphasizing the importance of the composition of the nutrient solution in affecting top-root ratios.

Cameron (5) and others have called attention to the fact that the relative proportion of mineral constituents has a marked effect on growth, causing tops to grow relatively faster than roots in some cases, at other times causing roots to make the more rapid growth.

The step from a plant like wheat or barley grown in a nutrient solution, to a deciduous orchard plant growing in the soil, is not an immediate one, but it might not be out of place to mention here some pruning results of Chandler (6) in so far as they concern the ratio of top to root growth in certain orchard trees. He gives data supporting the following statements:

> While the nitrate has increased both top and root growth, it has not increased root growth to as large an extent as it has increased top growth. Thus, while the top growth of fertilized trees [peaches] is twice as great as that of the unfertilized trees, the root growth is only 50 percent greater.

STATEMENT OF THE PROBLEM

It is clear from the foregoing brief discussion and review of literature that the few investigations reported up to the present time which deal with top-root growth ratios in plants as they are influenced by nutrient concentrations, give inconclusive results. It has not been possible to say with any degree of exactness just which one of several factors has been predominant in a given experiment. It has been found that water, temperature, light, and shade will influence top-root ratios; but this paper is confined to the effect of nutrient solutions. Miss Brenchley (3) has recently obtained some suggestive results by controlling the temperature factor in connection with nutrient cultures, and she shows how very important this factor is, especially with reference to the roots.

In view, therefore, of the scarcity of significant data, the writer has undertaken to investigate the influence of certain mineral nutrients in altering the ratio of top to root growth in certain plants and to suggest the probable mechanism underlying the resulting responses. This is a new field for specific investigation, and the solution of the problems involved offers much of value to the science of plant physiology, as well as to agricultural practice.

To a considerable extent, roots have specific nature and habits of their own apart from any characteristics which they may have as co-workers with tops for the good of the whole plant; they may be sharply polymorphic, as discussed later in this paper, and it has been suggested that they may behave at times as saprophytes when supplied with suitable carbohydrates, living at the expense of tops.

MATERIALS AND METHODS

Since these experiments were concerned with the effect of nitrates, a prerequisite at the outset was to devise a solution which would allow a wide variation in the nitrate ions without affecting very much the other essential elements necessary for favorable plant growth. One has ordinarily a wide choice in the selection of a nutrient solution; the general point of view, as gathered from a study of the solutions used by the various investigators and from their statements, is that there is no "best solution" nor specific ratio of ions or elements which will insure an optimum yield of plants under all conditions. Solutions, as mentioned already, which give optimum yield of roots, may not and often do not give optimum yield of tops, if by "optimum" we mean greatest green weight or dry weight.

It has been shown that, provided the total supply of mineral nutrients is adequate, the toleration of plants may extend over wide limits without significant falling off in yield.

The problem of varying nitrate ions for the present study without affecting greatly the other components was met by combining calcium nitrate, potassium nitrate, and magnesium nitrate as the source of nitrates; monobasic potassium phosphate, magnesium phosphate, and monobasic calcium phosphate as the source of phosphates; and magnesium sulphate, potassium sulphate, and calcium sulphate as the source of sulphates. The basic elements except iron are likewise derived from three different compounds. This really amounts to a three-salt solution. The following scheme will better enable us to visualize the component salts in the solution:

$Ca(NO_3)_2$	KNO_3	$Mg(NO_3)_4$
$Ca(H_2PO_4)_2$	KH_2PO_4	$Mg_3(PO_4)_2$
$CaSO_4$	K_2SO_4	$MgSO_4$

Reduction of salts in a horizontal or a vertical direction will enable us to vary the anions or cations at will. If a reduced or increased amount of nitrates is required in a particular solution, it may be secured by taking reduced or increased proportionate amounts of the three nitrate salts; while this will slightly reduce or increase, as the case may be, the total quantities of magnesium, calcium, and potassium in the solutions, the reductions or increments, being only a small part of the total amounts, would not greatly affect the total balance of these cations in the solution.[2] Care was observed always as to the total concentration.

In the first experiment, three solutions were employed; in these the quantities of nitrates were varied while the other components were kept approximately constant. This, of course, made a difference in the total concentration of the solutions, but the variations are well within limits which have been shown experimentally to be without significant effect upon yield.

The solution with the lowest nitrate concentration was designated Solution I; that next in order of concentration of nitrates, Solution II; and the one with the highest concentration of nitrates, Solution III. They had the following salt compositions:

	Sol. I (Low N)	Sol. II (Medium N)	Sol. III (High N)
KNO_3	.025 g.	.25 g.	.50 g.
KH_2PO_4	.1	.1	.1
K_2SO_4	.1	.1	.1
$Ca(NO_3)_2$	.025	.25	.50
$Ca(H_2PO_4)$	.1	.1	.1
$CaSO_4$	.1	.1	.1
$Mg(NO_3)_2$	.025	.25	.50
$Mg_3(PO_4)_2$	.1	.1	.1
$MgSO_4$	.1	.1	.1
H_2O	1,000 cc.	1,000 cc.	1,000 cc.
Total salts per liter	.675 g.	1.35 g.	2.1 g.

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[2] This method of varying the salt components was suggested by Dr. Otis F. Curtis and was found to be a much more practical way of varying the amounts of, or omitting, an element than the usual practice of substitution in which entirely new elements are often introduced or the concentration of certain of the other ions already present is greatly altered.

The concentrations employed, as seen above, were 675 p.p.m., 1,350 p.p.m., and 2,100 p.p.m. As ordinarily used, Pfeffer's solution contains 1,500 p.p.m.; Knop's, 1,400 p.p.m.; Crone's, 2,000 p.p.m.; and Sachs', 2,700 p.p.m. Solutions II and III as used in these experiments compare favorably in total salt concentration with those of Knop and Crone, respectively.

Baker's analyzed C.P. chemicals were employed. Each salt was dissolved separately in a proportionate part of distilled water, and these components were mixed as needed; when a salt was difficultly soluble it was added in the form of a suspension. Ferrous sulphate was used as the source of iron, and was added directly to cultures when set up, and at each change of solution, at the rate of .002 gram per liter.

The hydrogen-ion concentration of each solution was carefully checked by the colorimetric method each time solutions were prepared. In making up the standard solutions, Merck's specially prepared sodium phosphate and potassium phosphate, purified as specified by Sörensen, were used. The results were not compared finally with electrometric determinations, but by using overlapping indicators as suggested both by Prideau, and by Clarke and Lubbs, approximate accuracy was assumed.

There was some variation in the hydrogen-ion concentration from time to time; this was attributed to the varying states of purity in the monobasic calcium and potassium phosphates, different lots of which had to be used as the work progressed. However, the pH value at the beginning of the first experiment was 6.47; and the range was never greater than from 5.59 to 6.47.

The plants grew well in these solutions and produced, as far as could be judged from appearances, healthy tops and roots over a period of 56 days, the longest duration of any set of experiments.

Cultures were grown in the three solutions simultaneously. Mason fruit jars which have a capacity of about 1,000 cc. were employed as containers. The screw-top type of jar was found to be the most practical kind for this work. It has the advantage that discs of paraffined manila paper may be inserted in place of the glass cap, which can then be made fast by screwing the metal band down tightly. The discs, held in this way, make a firm and stable support for the growing seedlings, and the operation entails very much less labor than the usual method of fastening the paper with rubber bands, or setting the seedlings in slit cork stoppers. Wire supports were made fast around the neck of the jar for support of the seedlings as they grew. Four cultures of each solution with four plants to a culture constituted a series.

The seeds were germinated between moist blotting paper; when the radicles of seedlings to be used were about one inch in length, four holes were made through the paraffined discs with a clean, pointed glass rod, through which they were inserted into the solution.

The solutions were changed once a week, but distilled water was added every other day to make up for water which may have passed off through transpiration or evaporation. At the beginning of the experiments, it was thought advisable to change the solutions more frequently than once a week because of a possible exhaustion of nitrates, particularly in the low-nitrate solution; however, qualitative tests for nitrates by the diphenylamine method made at intervals of two days showed that this precaution was not necessary. All experiments were carried on in the greenhouse of the department of plant physiology of Cornell University.

After a series of preliminary experiments with different plants (including peas, corn, barley, buckwheat, and flax), barley was selected for the first work as it showed in comparison with the others the slightest apparent variation under greenhouse conditions; both the cultures as a whole and the individuals in a culture made a fairly uniform development.

The variety of barley used was known as Silver King; it was secured from Professor H. H. Love of the department of plant breeding and was a pure line which had been selfed for several generations.

It was assumed that any marked variations in growth would be due to the varying amounts of nitrate at the disposal of the plant, since the other components were approximately equal in the three solutions and since the plants grew in the greenhouse under the same external conditions of light, temperature, and relative humidity.

The general method employed for obtaining quantitative data was to harvest a series from each solution at the same stated time, to wash off any salt crystals that may have adhered, then to separate carefully tops from roots and desiccate them at a temperature of 102° C. to constant weight. Other features such as length and branching were sometimes taken into consideration. In later experiments green weights were also considered.

EXPERIMENTAL DATA

Experiment I

The duration of this experiment was 49 days. It was begun August 23, 1920. The first series was harvested at the expiration of 14 days, and another was taken down every seven days thereafter until all were removed.

Table 4 gives the comparative results of the six series conducted with barley. Since growth has been quite uniform, the culture has been taken as the unit for calculation. The ratios of tops to roots per culture have been computed, as well as the probable errors of the means of these ratios for each series. In some cases the difference between the means of the ratios has been given together with the probable error of these differences. This will serve to show the significance of results obtained by adding nitrates. As an aid in comparing the absolute efficiencies of the three solutions, total dry weights of the four cultures are given also.

In comparing the ratios of tops to roots for the 14-day period (table 4), it is to be noted that there is no significant difference between the mean of cultures of the low-nitrate and that of the medium-nitrate solutions. The mean of the solution with high nitrate, however, differs by a margin that is quite significant. The ratio is shown here to increase with the nitrate concentration of the solution, and it appears also that the effect may be noticeable during the early period of growth, even before the seedling has exhausted the supply of food stored within the endosperm.

When we compare the actual dry weights in this series, the growth values of tops in the higher-nitrate solution are found to be greatest; in fact, the top weights show a variation in proportion to the nitrate concentration of the solutions. This is not true of roots. Using dry weights of the lowest nitrate solution as a basis, the top weight in the high-nitrate solution shows an increase of 28 percent over that in the low-nitrate solution, while the root weight shows an increase of only 2 percent; in the medium-nitrate solution, tops and roots show increases of about 15 percent each.

The relative behavior of tops and roots of those plants harvested at the expiration of 21 days is still more striking than in the case of those harvested after 14 days. The increase in dry weight of tops in the high-nitrate solution over that in the low is 23 percent, while the corresponding increase for roots is only .3 percent. Comparing these figures with 28 percent and 2 percent respectively in the preceding series, it becomes clear that roots are not being influenced in any such positive way by the nitrate treatment as tops. The medium-nitrate solution gives an increase of 13 percent and 10 percent respectively for tops and roots over the corresponding parts in the low-nitrate solution. This solution is regarded as the best balanced of the three and should show, therefore, more normal relationships between tops and roots.

Series 3 was harvested after 28 days' growth; significant differences are clearly shown between the ratios expressing the variation between different stages of maturity, as well as between the ratios of tops to roots in the different solutions. Notwithstanding the differences in mean ratio, there is not a striking difference between the total weights of cultures (tops and roots) of the different solutions, as a study of the table will show. This would indicate, of course, that the growth-producing values of the solutions do not differ very much.

Another interesting fact shown in Series 3 is that while ratios of tops to roots have increased steadily with the nitrate concentration of the solution, the actual dry weights of roots in the medium- and high-nitrate solutions have now become less in value than those of roots in the low-nitrate solution, and this relationship continues during the rest of the experiment.

The results of Series 4, 5, and 6 are given in table 4. They were harvested after 35, 42, and 49 days respectively, and bring out substantially the same facts which have been already emphasized, namely, that at all stages there is an increase in ratio of tops to roots as the nitrate content is increased.

In addition to the unmistakable evidence given as to the effect of increasing the nitrate concentration in the solution, as a study of the probable errors of the differences will show, attention might be called again, in Series 6, to the absolute dry weight of roots in the low-nitrate solution (1.8131 grams) and in the high-nitrate solution (1.1687 grams). The production of tops has been greatest in the medium-nitrate solution, as has been true throughout. If we now add total dry weights again for each of the three solutions, the interesting fact stands out that there is not a great difference in the total growth-producing value. The medium-nitrate solution is most efficient, with a total production of 13.2377 grams, followed by the high-nitrate solution with 11.7172 grams, and the low-nitrate solution with 11.4555 grams. The two latter solutions have about the same total efficiency, yet the ratio of tops to roots is strikingly different, the difference of the means being 3.75 ± .238, or about 70 percent.

Increase in Ratio of Tops to Roots as Plants Grow Older

The ratio of tops to roots increased both with nitrate concentration of the solution and with increased age. The normal increase of this ratio with age has not been adequately considered heretofore in the literature, and as yet the exact mechanism underlying this phenomenon awaits rational explanation. Table 4*a* gives data showing the increase with age; while the increases are quite significant in the low-nitrate solution, they are strikingly so in the medium- and high-nitrate solutions.

Growth Features

Quantitative data were not recorded as to transpiration or length of tops in Experiment I, but notes kept throughout the time the plants were growing show very little difference either in greenness or in height of tops. Plants grown in the low-nitrate solution were somewhat more slender, but appeared always more turgid. The aging or dying of the first or oldest leaf is not without interest. In the present experiment, as well as in the preliminary ones with barley, gradual dying of the lower leaf beginning with the tip started first with plants in the high-nitrate solution and would not begin in the low-nitrate solution until two or three weeks later.

The longest roots occurred in the high-nitrate solution. These were less branched, and the root system appeared, therefore, more slender than those in the other two solutions. It was particularly noticeable that aërial roots were scarcely formed at all in the high-nitrate cultures, while they developed abundantly in the others. The less abundant production of lateral roots in the high-nitrate solution as found here is in contrast to Müller-Thurgau's finding that the presence of nitrogen in a solution causes a much more vigorous growth of secondary roots.

As cultures grew in the greenhouse, they would be attacked during the later stages by *Erysiphe graminis;* the high-nitrate cultures were particularly susceptible to this fungus and could be readily picked out from the others by this fact. Medium-nitrate cultures were not so badly affected, and the low-nitrate cultures scarcely at all. This susceptibility to the fungus, varying with the nitrate concentration in the nutrient solution, was constant for the three sets of experiments conducted with barley and was independent of the total concentration. There seems to be a direct relation between the nitrate concentration and the plant's susceptibility to the fungus in question. Experiments are being conducted to throw some light on the mechanism of this relationship.

TABLE 4. *Experiment I (Barley); Ratio of Tops to Roots as Nitrate Concentration is Increased (Dry Weights in Grams)*

	Sol. I (Low Nitrate)			Sol. II (Medium Nitrate)			Sol. III (High Nitrate)		
	Tops	Roots	Tops/Roots	Tops	Roots	Tops/Roots	Tops	Roots	Tops/Roots
Series 1, *14 days*	.2145 .1606 .1830 .1620	.0644 .0510 .0517 .0525	3.33 3.15 3.54 3.09	.2180 .2000 .1960 .2135	.0690 .0627 .0524 .0670	3.159 3.189 3.740 3.186	.2462 .2320 .2179 .2234	.0635 .0512 .0583 .0510	3.88 4.53 3.74 4.38
Total ..	.7201	.2196		.8275	.2511		.9195	.2240	
Mean..			3.28±.068			3.32±.095			4.13±.129

Difference......................High Nitrate − Medium Nitrate = .81 ± .160.

Series 2, *21 days*	.3079 .3525 .4691 .3882	.0722 .0845 .1074 .0953	4.26 4.17 4.37 4.07	.4266 .4287 .4487 .4045	.1008 .1050 .1030 .0861	4.23 4.08 4.36 4.70	.4500 .5591 .5000 .3625	.0813 .1105 .0979 .0709	5.53 5.06 5.11 5.11
Total ..	1.5177	.3594		1.7085	.3949		1.8716	.3606	
Mean..			4.22±.0431			4.34±.088			5.20±.074

Difference......................High Nitrate − Medium Nitrate = .86 ± .115.

Series 3, *28 days*	.8500 .7645 .6814 .8697	.1889 .1700 .1552 .2121	4.50 4.49 4.39 4.10	.9100 .8155 .8965 .9175	.1675 .1573 .1770 .1878	5.43 5.12 5.07 4.89	.9500 .9200 .8880 .8251	.1700 .1477 .1500 .1559	5.59 6.23 5.92 5.29
Total ..	3.1656	.7262		3.5395	.6896		3.5831	.6236	
Mean..			4.37±.063			5.13±.076			5.75±.136

Difference........................High Nitrate − Low Nitrate = 1.38 ± .149.

TABLE 4 (*Continued*)

Series 4, *35 days*	1.2889	.2600	4.95	1.3420	.2026	6.62	1.4853	.2200	6.75
	1.2836	.2864	4.48	1.5517	.2233	6.94	1.4250	.2145	6.64
	1.2500	.2386	5.24	1.5643	.2381	6.56	1.1300	.1568	7.21
	1.1891	.2333	5.09	1.2883	.2099	6.13	1.3756	.2000	6.87
Total ..	5.0116	1.0183		5.7463	.8739		5.4159	.7913	
Mean..			4.94 ± .111			6.56 ± .102			6.87 ± .083

Difference........................High Nitrate − Low Nitrate = 1.93 ± .138.

	Sol. I (Low Nitrate)			Sol. II (Medium Nitrate)			Sol. III (High Nitrate)		
	Tops	Roots	Tops / Roots	Tops	Roots	Tops / Roots	Tops	Roots	Tops / Roots
Series 5, *42 days*	1.9081	.4140	4.61	2.4047	.3131	7.70	2.0086	.2588	7.76
	1.6279	.3344	4.87	1.9157	.2387	8.02	1.7675	.2263	7.81
	1.6866	.3025	5.58	2.0000	.2700	7.41	2.1588	.3072	7.03
	1.8381	.3735	4.90	2.0960	.2717	7.71	1.9140	.2384	8.03
Total ..	7.0607	1.4244		8.4161	1.0935		7.8489	1.0307	
Mean..			4.99 ± .139			7.71 ± .084			7.66 ± .146

Difference........................High Nitrate − Low Nitrate = 2.67 ± .201.

Series 6, *49 days*	2.5525	.4710	5.42	2.8500	.3243	8.79	2.7418	.3200	8.56
	2.3430	.4397	5.33	3.0170	.3619	8.33	3.2016	.3600	8.89
	2.3285	.4180	5.57	3.2385	.3952	8.19	2.1793	.2168	10.05
	2.4184	.4844	4.99	2.7052	.3456	7.82	2.4268	.2719	8.81
Total ..	9.6424	1.8131		11.8107	1.4270		10.5495	1.1687	
Mean..			5.33 ± .082			8.28 ± .135			9.08 ± .224

Difference........................High Nitrate − Low Nitrate = 3.75 ± .238.

TABLE 4*a*. *Increase in Ratio of Tops to Roots in Young Barley Plants at Different Stages of Maturity*

(*Average of 4 Cultures, 4 Plants to a Culture*)

		14 Days	21 Days	28 Days	35 Days	42 Days	49 Days
Low Nitrate: Tops / Roots...	Mean.	3.28 ± .068	4.22 ± .043	4.34 ± .063	4.94 ± .111	4.99 ± .139	5.33 ± .082
	Diff. .		.94 ± .080	.12 ± .076	.60 ± .127	.05 ± .177	.34 ± .161
Medium Nitrate: Tops / Roots...	Mean.	3.32 ± .095	4.34 ± .088	5.13 ± .076	6.56 ± .102	7.71 ± .084	8.28 ± .135
	Diff. .		1.02 ± .129	.79 ± .116	1.43 ± .127	1.15 ± .132	.57 ± .157
High Nitrate: Tops / Roots...	Mean.	4.13 ± .129	5.20 ± .074	5.75 ± .136	6.87 ± .083	7.66 ± .146	9.08 ± .224
	Diff. .		1.07 ± .148	.55 ± .150	1.12 ± .157	.79 ± .168	1.42 ± .267

Experiment II

Behavior of Nitrates when Total Concentrations are Reversed

In the foregoing experiment the three solutions differed in total concentration as well as in the concentration of nitrates. It happened that the solution with the highest nitrate content had also the highest total concentration. The question is naturally raised, then, as to whether or not the increased concentration of the solution rather than the increased nitrate content is responsible for the increased ratio of tops to roots. This question has led to the arranging of a second experiment in order to throw light on this phase of the problem. It is recalled here that Stiles and Miss Brenchley found that the top-root ratios decreased as the concentration was decreased.

For this experiment, Solution II (medium nitrate) remained as in Experiment I. The low-nitrate solution is modified and designated Solution I*a*. In this, the nitrate content is kept the same, but the other salt components are increased to .5 gram per liter, which makes the modified solution about 5 times the original, Solution I. The high-nitrate solution is designated Solution III*a*; it likewise retains the same amount of nitrate as before, but the remaining six salts are reduced to .06 gram each, thereby reducing the total concentration of the solution about one seventh. The composition of the solutions used in Experiment II was as follows:

	Sol. I*a* (Low Nitrate)	Sol. II (Medium Nitrate)	Sol. III*a* (High Nitrate)
KNO_3	.025	.25	.5
KH_2PO_4	.5	.1	.06
K_2SO_4	.5	.1	.06
$Ca(NO_3)_2$	.025	.25	.5
$Ca(H_2PO_4)_2$	.5	.1	.06
$CaSO_4$	.5	.1	.06
$Mg(NO_3)_2$	.025	.25	.5
$Mg(PO_4)_2$	.5	.1	.06
$MgSO_4$	.5	.1	.06
Total	3.075	1.35	1.86

The highest concentration here is somewhat above that of Sachs' solution mentioned above. The newly made solutions had the following pH values: Sol. I*a*, 5.59; Sol. II, 6.24; Sol. III*a*, 6.24. Iron was supplied as in Experiment I.

Twenty cultures were set up for each solution in the same manner as previously described. Four of these, constituting a series, were harvested every two weeks. The solutions were changed weekly, but were filled up every day to make up for water lost. The experiment began October 28, 1920, and ran for 56 days. Dry weights only are recorded.

Weather conditions throughout the duration of this experiment were not favorable for plant growth; the continual cloudiness together with the late autumn season made for much less growth in this set of experiments than occurred in Experiment I. These conditions are taken to account for the unsteadiness of growth which is shown from a study of the actual dry-weight values, as well as from a study of the magnitude of the probable errors of the mean ratios of tops to roots which have been computed in each case. The results of the four series of Experiment II are given in table 5.

It will be remembered that the low-nitrate solution now contains 3,075 p.p.m.; the medium-nitrate, 1,350 p.p.m., and the high-nitrate, 1,860 p.p.m. The ratios of tops to roots do not appear to be affected appreciably by the concentrations of the solutions; for in this experiment we have not simply the reverse conditions as to concentration, but the total concentration of the low-nitrate solution is now nearly 5 times its former value, yet results obtained throughout the four series are uniformly comparable to those obtained in Experiment I. The significance of the data obtained in this experiment is clearly shown from a study of the differences of the means of the ratios of the different solutions, taking into consideration the probable errors (table 5). Concentration as such, therefore, has shown no effect upon the ratio of tops to roots.

Growth Features

Root growth of cultures in Solution I*a* (3,075 p.p.m.) was of a different character from that in the two other, less concentrated solutions. The roots are much shorter, more turgid, and the individual fibers are greater in diameter. Data for length of tops and roots taken for the first three series are as follows:

		Sol. I*a* (Low Nitrate)	Sol. II (Medium Nitrate)	Sol. III*a* (High Nitrate)
Series 1	Tops	15.2 cm.	18.3 cm.	16.2 cm.
	Roots	7.75 "	16.0 "	16.2 "
Series 2	Tops	37.88 "	34.25 "	34.5 "
	Roots	9.28 "	18.5 "	19.5 "
Series 3	Tops	40.9 "	39.5 "	41.6 "
	Roots	11.1 "	19.1 "	17.0 "

The length of tops continues about the same during these three series. No differences were observed as to health and vigor of these cultures, so the effect of this more highly concentrated solution seems to be shown in bringing about a change in the morphological character of the root. Since the growth values in this solution relative to the medium-nitrate solution (which is the same as that used in Experiment I, both as to nitrate concentration and as to total concentration) and in Solution III*a* are practically the same as they were where we had the reverse concentration conditions, it would seem that the physiological processes underlying this change are of a different order and, being within the root itself, do not affect the ratio of tops to roots. Another fact indicated is that there is probably a critical concentration of solution beyond which the root will respond morphologically more or less sharply; evidence for this is shown from the data that the longest roots were in the high-nitrate solution in Experiment I, which had a concentration of 2,100 p.p.m., while with a concentration of 3,075 p.p.m. they are shortest and are otherwise different in form.

Increase in Ratio of Tops to Roots at Different Stages of Maturity in Young Plants

Table 5*a* shows the increase in the ratio of tops to roots, at different stages of maturity as the plants grew under the conditions of this experiment. This table shows results similar to those secured in Experiment I.

TABLE 5. *Experiment II (Barley); Behavior of Nitrates when Total Concentration is Reversed (Dry Weights in Grams)*

	Sol. I*a* (Low Nitrate)			Sol. II (Medium Nitrate)			Sol. III*a* (High Nitrate)		
	Tops	Roots	Tops / Roots	Tops	Roots	Tops / Roots	Tops	Roots	Tops / Roots
Series 1, *14 days*	.0437	.0135	3.23	.0883	.0200	4.41	.0632	.0163	3.94
	.0559	.0183	3.05	.0758	.0188	4.03	.0654	.0146	4.47
	.0587	.0182	3.23	.0740	.0178	4.15	.0624	.0160	3.90
	.0650	.0182	3.57	.0710	.0164	4.34	.0624	.0150	4.16
Total ..	.2233	.0682		.3091	.0730		.2534	.0619	
Mean..			3.27 ± .073			4.32 ± .058			4.12 ± .088
Difference........................	High Nitrate − Low Nitrate = .85 ± .114.								
Series 2, *28 days*	.1500	.0313	4.19	.1841	.0322	5.72	.1867	.0290	6.44
	.1430	.0263	5.43	.2040	.0320	6.38	.1792	.0270	6.64
	.1733	.0346	5.00	.1643	.0263	6.21	.2085	.0295	7.07
	.1462	.0340	4.30	.2122	.0329	6.45	.1795	.0290	6.23
Total ..	.6123	.1262		.7646	.1244		.7539	.1145	
Mean..			4.88 ± .157			6.19 ± .111			6.59 ± .122
Difference........................	High Nitrate − Low Nitrate = 1.71 ± .199.								
Series 3, *40 days*	.3310	.0707	4.70	.3370	.0478	7.05	.4020	.0526	7.64
	.2586	.0577	4.48	.4529	.0651	6.96	.4616	.0525	8.79
	.2810	.0600	4.68	.4917	.0715	6.88	.4213	.0562	7.49
	.3308	.0600	5.51	.3938	.0622	6.33	.5308	.0671	7.91
Total ..	1.2014	.2484		1.6754	.2466		1.8157	.2284	
Mean..			4.84 ± .153			6.81 ± .108			7.95 ± .122
Difference........................	High Nitrate − Low Nitrate = 3.11 ± .195.								

TABLE 5—*Continued.*

Series 4, *56 days*	.7350 1.0361 .5730 .9527	.1257 .1571 .0943 .1772	5.84 6.59 6.07 5.38	1.3527 1.3000 1.1826 1.1953	.1334 .1280 .1418 .1600	10.14 10.15 8.34 7.47	1.3164 1.3200 1.2264 1.2432	.1611 .1350 .1172 .1238	8.11 9.77 10.46 10.04
Total ..	3.2968	.5543		5.0306	.5632		5.1160	.5371	
Mean..			5.97±.169			9.03±.454			9.59±.347

Difference........................High Nitrate − Low Nitrate = 3.62 ± .386.

TABLE 5*a*. *Experiment II; Increase in Ratio of Tops to Roots in Young Barley Plants at Different Stages of Maturity*

(*Averages of 4 Cultures, 4 Plants to a Culture*)

		14 Days	28 Days	40 Days	56 Days
Low Nitrate:					
$\frac{\text{Tops}}{\text{Roots}}$..........	Mean.........	3.27±.073	4.88±.157	4.84±.153	5.97±.169
	Diff...........		1.61±.173		1.13±.228
Medium Nitrate:					
$\frac{\text{Tops}}{\text{Roots}}$..........	Mean.........	4.23±.05	6.19±.111	6.81±.108	9.03±.454
	Diff...........		1.96±.125	.62±.154	2.22±.466
High Nitrate:					
$\frac{\text{Tops}}{\text{Roots}}$..........	Mean.........	4.12±.088	6.59±.122	7.95±.122	9.59±.347
	Diff...........		2.47±.150	1.36±.172	1.64±.368

Experiment III

Effect of Nitrates upon Ratio of Tops to Roots in Corn Plants

In order to get comparative data as to the effects of nitrates, Experiment III was conducted with corn. A selected variety of field corn was used. The method was practically the same as that used for barley. Three corn seedlings were employed to a culture and three cultures constituted a series. The first series was removed at the end of 27 days, the second at the end of 34 days, and the third at the end of 41 days. Both green and dry weights of tops and roots are recorded, as are also the probable errors of the means of the dry-weight ratios. It was found practicable in this experiment to use two solutions only, the low-nitrate and the medium-nitrate solutions.

The results are given in table 6. The difference between the ratios of tops to roots is not significantly large for the first series; this was true also of the first series with barley, and indicates that the seedling is influenced more greatly by the composition of the solutions after the tops have begun to function actively. The second series, however, gives a difference in favor of the medium-nitrate solution of 1.88 ± .261, and the third series a difference of 3.34 ± .678, as will be seen from the table.

The increase in ratio of tops to roots as the plants grow older is brought out in this experiment, as was the case for barley in Experiment I. Thus the results of Experiment III confirm in every way those obtained with barley. The three experiments leave no doubt as to the effect of nitrates in increasing the ratio of tops to roots in these two plants under the conditions employed.

It is worthy of note, also, that there is little difference in the efficiencies of these two solutions as measured by total growth produced either in green or in dry weight.

			(Green Wt.)	(Dry Wt.)
In Series 1,	Sol. I,	Total Growth	39.3199	3.8014 (low nitrate)
	Sol. II,	" "	36.9930	3.2390 (medium nitrate)
In Series 2,	Sol. I,	" "	49.4250	4.8440
	Sol. II,	" "	54.6613	4.4670
In Series 3,	Sol. I,	" "	61.4600	5.7998
	Sol. II,	" "	61.5000	5.5905

These figures show that plants in the higher-nitrate solution have relatively higher water contents and correspondingly smaller dry weights. In the light of this fact, there is great need of more careful consideration than is usually given as to what one desires of the plant before concluding as to the effectiveness of a particular solution or a particular fertilizer; also, dry-weight determinations which are not checked up occasionally with the green weights may be wholly misleading as to the actual amount of growth which may have taken place during a given period.

Growth Features

This was not a very favorable season for growing corn (February 1–March 13), hence growth was slow, though the plants showed no external evidence either in tops or in roots of not being entirely healthy. No particular differences were noticeable in height or color of tops, but the roots in the low-nitrate solution were notably longer and larger from the first series (table 6).

Experiment IV

Effect of Increasing the Concentration of Nitrates upon the Ratio of Tops to Roots in Flax

In the course of preliminary experiments, it was noticed that the ratios of tops to roots in certain plants were not appreciably altered by increasing the nitrate concentration of the solution. One of these plants was flax. Experiment IV was conducted, therefore, with flax to get more data on this point. A seed type of flax was used, one which had been selfed for several generations, thus assuring a certain grade of stability.

The plants grew 41 days in the greenhouse simultaneously with the corn in Experiment III. They were green and healthy throughout, but

TABLE 6. *Experiment III (Corn); Ratio of Tops to Roots as Nitrate Concentration is Increased (Green and Dry Weights in Grams)*

		Series 1—27 Days			Series 2—34 Days			Series 3—41 Days		
		Tops	Roots	Tops/Roots	Tops	Roots	Tops/Roots	Tops	Roots	Tops/Roots
Sol. I (Low Nitrate)	Green Wt...	8.8069	2.6230		11.1420	2.482		17.7100	3.9100	
		10.6200	3.9400		14.3820	3.9250		17.4800	4.8300	
		10.8150	2.5150		14.6120	2.6820		14.4400	3.0900	
	Total.......	(30.2419)	(9.0780)		40.3360	9.0890		49.6300	11.8300	–
	Dry Wt.....	.8760	.2033	4.31	1.1300	.2000	5.65	1.3416	.2511	5.34
		1.1141	.2900	3.84	1.4760	.2840	5.20	1.9318	.3000	6.43
		1.1060	.2120	5.21	1.5130	.2410	6.27	1.7420	.2333	7.46
	Total......	(3.0961)	(.7053)		4.1190	.7250		5.0154	.7844	
	Mean......			4.44±.261			5.71±.211			6.41±.407
Sol. II (Med. Nitrate).......	Green Wt...	10.7390	2.1548		16.9420	1.7134		19.1500	2.9000	
		9.8600	2.4342		16.6519	2.3700		15.1000	2.4400	
		10.0550	1.7600		14.9600	2.0240		19.0000	2.9100	
	Total......	(30.6540)	6.3490		(48.5539)	(6.1074)		53.2500	8.2500	–
	Dry Wt.....	.9132	.1900	4.81	1.3900	.1800	7.72	1.9316	.1662	11.63
		.8670	.1864	4.65	1.3060	.1650	7.91	1.4852	.1611	9.22
		.9239	.1795	5.15	1.2520	.1740	7.14	1.5964	.1900	8.40
	Total.......	(2.7041)	(.5559)		(3.9480)	(.5190)		(5.0132)	.5173	
	Mean.......			4.87±.099			7.59±.056			9.75±.675

Difference........................Medium N. – Low N. = 1.88 ± .261. Medium N. – Low N. = 3.34 ± .678.

those in the low-nitrate solution seemed slightly more vigorous and had slightly longer tops for each series, as well as longer roots. The lengths of tops and roots are given for two series:

		Sol. I (Low N.)	Sol. II (Med. N.)	Sol. III (High N.)
Series 2 (36 days)	Tops	19 cm.	17.5 cm.	17.5 cm.
	Roots	26.3 "	20 "	18.3 "
Series 3 (41 days)	Tops	21.3 "	19.6 "	19.3 "
	Roots	28.6 "	26.5 "	18.5 "

Table 7 gives the green weights and dry weights obtained in this experiment. It will be noticed that this plant makes no appreciable response, in the ratio of tops to roots, to increased nitrate content of the solution. In other words, it would seem that in the case of flax we are dealing with a plant of an entirely different physiological constitution in so far as its ability to utilize nitrates is concerned. To what range it might respond, the limits of this experiment have not permitted investigation, but this fact presents a very interesting problem from the standpoint of flax nutrition (table 7).

Studies to Determine the Direct Effect of Nitrates upon Root Growth by Growing Roots of Certain Plants in Pure Cultures

Data submitted in the foregoing experiments show conclusively that concentration of nitrate ions in the nutrient solutions used, regardless of the total salt concentration of the solution, was the determining factor in altering the ratios of top growth to root growth in barley and corn. These experiments do not give evidence, however, as to how this alteration comes about. The writer has, therefore, carried out another set of experiments with the hope of finding out whether nitrates check the growth of roots directly, or whether the greater ratio of tops to roots as well as the actual reduction in root growth in the higher-nitrate solution may be due chiefly to processes set up in the tops which affect the distribution of food between tops and roots.

Several methods were followed in this phase of the work. The effort was centered chiefly in removing the influence of tops and noting the effect of different treatments upon roots.

For these experiments, the same high-, medium-, and low-nitrate mineral nutrient solutions were employed as in Experiment I, but to each solution glucose was added at the rate of 2 grams per 100 cc. of solution, to supply the carbohydrate which normally comes from the leaves.

The cultures were grown singly in 250-cc. globe flasks, or in some cases in Erlenmeyer flasks, in 100 cc. of solution. The cleaned culture flasks

TABLE 7. *Experiment IV (Flax); Ratio of Tops to Roots as Nitrate Concentration is Increased (Green Wt. and Dry Wt. in Grams)*

		Series 1—21 Days			Series 2—36 Days			Series 3—41 Days		
		Tops	Roots	Tops/Roots	Tops	Roots	Tops/Roots	Tops	Roots	Tops/Roots
Sol. I (Low Nitrate)	Green Wt.	0.8737 1.0359 0.7751	.3546 .5120 .3400		4.4100 4.2600 4.6400	1.5100 1.5100 1.5850		4.8100 4.9350 5.9150	1.2700 1.2300 1.5400	
	Total	2.6847	1.2066		13.3100	4.6050		15.6600	4.0400	
	Dry Wt.	.1173 .1283 .1055	.0433 .0476 .0388		.4940 .4840 .5340	.1210 .1130 .1200		.6800 .6775 .8210	.1580 .1700 .1878	
	Total	.3511	.1297		1.5120	.3540		2.1785	.5158	
	Mean			2.7			4.2			4.2
Sol. II (Med. Nitrate)	Green Wt.	.5140 .6960 .6326	.2122 .2347 .1421		3.5700 3.2000 3.5300	1.4100 .9800 1.1750		4.9150 4.8978 4.3900	1.3800 1.4830 1.3916	
	Total	1.9026	.5890		10.2400	3.5650		14.2028	4.25466	
	Dry Wt.	.0600 .0845 .0900	.0245 .0335 .0358		.3850 .3520 .4130	.0940 .0830 .1000		.6770 .6520 .5810	.1740 .1654 .1533	
	Total	.2345	.0938		1.1500	.2770		1.9100	.4927	
	Mean			2.5			4.18			3.87
Sol. III (High Nitrate)	Green Wt.	.4614 .6041 .5379	.0768 .1000 .0890		3.5000 3.1520 3.5700	1.2100 1.0900 1.1300		5.0500 5.7168 4.3000	1.7450 1.7750 1.3060	
	Total	1.6034	.2658		10.2220	3.4300		15.0668	4.8260	
	Dry Wt.	.0559 .0715 .0674	.0220 .0300 .0266		.4200 .3900 .4350	.0950 .0980 .1040		.6869 .7668 .5725	.1649 .1659 .1416	
	Total	.1948	.0786		1.2450	.2970		2.0262	.4724	
	Mean			2.5			4.2			4.29

containing the solutions were plugged with cotton and sterilized for 30 minutes at 15-pounds' steam pressure.

Seeds

The seeds for the cultures were carefully selected on the basis of their vigor and uniformity. They were first sterilized for 4 hours by the calcium hypochlorite method developed by Wilson (34) in 1915, and after being washed with sterile water they were transferred for germination to sterile agar in plugged 50-cc. vials. A word might be said here with reference to the Wilson solution as a sterilizing medium. A claim for this method which would highly recommend it is that seeds may be effectively transferred from it directly to the germinating medium without washing in sterile water. When one is dealing with individually weighed and recorded seeds, the percentage germination of these seeds becomes a very important factor both from the standpoint of accuracy of results and from that of labor involved. It is the writer's experience that unless the grains of corn are washed thoroughly on transference from the calcium-hypochlorite solution to an agar germinating medium, the percentage of germination is greatly reduced, sometimes as much as 60 percent.

Cultures were grown in the greenhouse in a dark chamber specially constructed to allow for the free circulation of air.

In Experiment V, the tips only of corn roots were employed. When the radicle had reached a length of 2 to 3 cm., it was removed with a sharp scalpel, under sterile conditions, dropped into the sterile culture solution, and set away in the dark chamber for growth.

The results of two series of 20 and 44 days' growth respectively are presented in table 8. A third series was conducted, but as several cultures in the low- and medium-nitrate solutions became contaminated, comparative results are not possible, though the results in the high-nitrate solution both as to green and as to dry weight are essentially the same as those reported in Series 1. Eight cultures constituted a series.

The results of Series 1 (Experiment V), in which root tips only were used, show clearly, as far as green-weight determinations are concerned, that there is an increase in weight when the amount of nitrates in the solution is increased. The medium-nitrate solution appears slightly more efficient here, as was the case with cultures of entire plants growing in the mineral-nutrient solutions alone.

The dry-weight determinations for the twenty-day period do not, at first glance, appear to give such positive evidence as those of green weight of an increased growth as the nitrate content of the nutrient solution is increased, since there are such small differences among the weights for this period; but the fact has already been demonstrated and pointed out that dry-weight determinations are by no means safe criteria of growth of plants

TABLE 8. *Experiment V; Effect of Increasing Nitrates on Growth of Root Tips of Corn (Dry Weights in Grams)*

	Sol. I (Low Nitrate), Roots			Sol. II (Medium Nitrate), Roots			Sol. III (High Nitrate), Roots		
	Green Wt.	Dry Wt.	Length	Green Wt.	Dry Wt.	Length	Green Wt.	Dry Wt.	Length
Series 1, *20 days*...	.1100	.0069		.1158	.0100		.1172	.0077	
	.0895	.0080		.2006	.0130		.1334	.0076	
	.1769	.0214		.0852	.0060		.1071	.0059	
	.2153	.0196		.2217	.0077		.1493	.0124	
	.1202	.0096		.1252	.0157		.1613	.0126	
	.1576	.0142		.1515	.0100		.1775	.0102	
	.1777	.0062		.2108	.0125		.1592	.0130	
	.1625	.0082		.1331	.0128		.1248	.0089	
Mean............	.1262±.0124	.0118±.0014	18.8 cm.	.1555±.0119	.0110±.00075	18.6 cm.	.1475±.0057	.0098±.00064	21.2 cm.
	Dry Wt.			Dry Wt.			Dry Wt.		
Series 2, *44 days* ..	.0202		43.2	.0166		40.5	.0045		26.5
	.0255		50.0	.0326		41.2	.0104		37.0
	.0109		27.0	.0251		54.0	.0131		44.5
	.0116		20.0	.0231		30.0	.0051		21.5
	.0134		28.0	.0082		27.0	.0094		33.0
	.0119		25.5	.0067		22.5	.0047		20.5
	.0141		16.0	.0086		31.5	.0089		22.0
	.0097		28.5	.0087		30.5	.0135		47.5
Mean............	.01466		28.5 cm.	.0162		34.65 cm.	.0087		31.5 cm.

when grown under different environmental conditions. Those plants which had a higher nitrate substrate for growth had a relatively smaller dry-matter content, while the reverse is true with those having less nitrates available. This is clearly brought out in the figures under consideration (table 8), and more clearly still in table 10. It would appear that metabolic processes such as respiration—not accompanied by increase in dry matter, but accompanied by an accumulation of aqueous or other volatile material—are accelerated in consequence of the larger available supply of nitrates. Physically, plants growing under such conditions take on the character of greater succulency.

The green weights were not determined for the 44-day-period cultures, but the dry weights are essentially as in Series 1, with a relatively higher dry-matter content for the low-nitrate cultures and a strong indication of an increased utilization of food in respiratory processes in the cultures in the high-nitrate solution.

Measurements were made of length of roots for the 20- and 44-day periods respectively in order to determine whether or not the differences in nitrate content of the solutions had any stimulating effect on length. While the average lineal growth is somewhat higher in solutions with larger nitrogen content, the difference is not large enough to be significant (table 8). It is interesting, however, to note that these root tips have continued to grow through a period of 44 days, increasing considerably in length, as is shown in the table, but showing little or no increase in total dry matter.

Experiment VI

Effect of Increased Nitrates upon Growth in Length of Isolated Tips of Radish Roots

Germination of the seeds and preparation of the root tips for these cultures were carried out in the same manner as that described for corn. The cultures ran for 15 days.

The results are given in table 9. They show no striking response in length of root of this plant to the increased nitrate content of the solution.

TABLE 9. *Radish; Results of 15 Days' Growth (Lengths in Centimeters)*

Culture	Solution I (Low N.)	Solution II (Medium N.)	Solution III (High N.)
1	9	12	9.5
2	7	7.3	6.3
3	5	20.5	12.5
4	7.5	13.5	8
5	11	6	8
Mean	8	11.8	8.8

Experiment VII

Effect of Increased Nitrates upon Growth of Roots of Corn with Plumule and Endosperm Removed, but with Cotyledon Attached

The cultures for this experiment were set up in exactly the same manner as that described for Experiment V, with the exception that the corn roots used had the cotyledon attached. The plumule and the endosperm were both removed under sterile conditions. Both green and dry weights are recorded in table 10. Two series were conducted, with 8 individual cultures to a series. Each series grew for twenty days. At the end of the growth period the remains of the cotyledon were removed, when the green and dry weights were determined.

A study of the two series shows an unmistakable increase in growth in the roots grown in solutions with higher nitrate content. This is more obvious in the green weights than in the dry weights. It is to be expected that the dry weight would be relatively less in the high-nitrate solution, for the more vigorous growth would be attended by more active respiratory processes which would consume much of the food that would otherwise be left for building material. Comment upon this table is hardly necessary. The probable errors of the differences, while apparently not so significant for the dry weights, are clearly so for the green weights. The greater succulency, as has already been mentioned, of the plants growing in the higher-nitrate solutions is a factor to be considered carefully in connection with the differences in dry weight between these and the lower-nitrate cultures.

Several series of experiments were carried out by growing plants in mineral nutrients both in the light and in the dark chamber, with plumules removed, but the results were wholly negative as to any effects of nitrates directly upon the roots.

Discussion

The experiments reported in this paper show clearly that increasing the nitrate concentration of a nutrient solution, within the range investigated, will increase the ratio of top growth to root growth in certain plants. In some cases this alteration of ratio is attended with very little difference in the total yield of the different solutions used.

In the literature, attention has been given to some extent to the effect of differences in total concentration upon the ratio of tops to roots, but no work of controlled nature has been done hitherto to detect and to localize the cause of specific effects of particular mineral nutrients on this ratio.

The results of Experiments I and II bring out the fact that concentration as such is without effect, but that the composition of the solution is the factor of most importance. This work confirms the conclusions of Cameron (5), Hoagland (15), Shive (28), and Duggar (9) with respect to placing

TABLE 10. *Experiment VII; Effect of Increasing Nitrates on Growth of Root Tips of Corn (Green and Dry Weights in Grams)*

	Sol. I (Low Nitrate), Roots		Sol. II (Medium Nitrate), Roots		Sol. III (High Nitrate), Roots	
	Green Wt.	Dry Wt.	Green Wt.	Dry Wt.	Green Wt.	Dry Wt.
Series 1, *20 days*	.5187	.0905	1.5181	.1749	.8229	.0875
	.3502	.0926	.8762	.0950	.7495	.0663
	.6724	.1116	1,2913	.1199	.7012	.0634
	.4435	.0766	1.1171	.1238	.5088	.0640
	.6469	.1054	.5605	.0783	1.1619	.1180
	.3624	.0673	1.3884	.1459	2.1832	.1765
	.2209	.0448	.4510	.0548	1.8442	.1584
	.2100	.0390	.5336	.0812	1.0061	.0968
Mean	.4369±.0413	.0785±.0064	.9670±.0890	.1092±.0093	1.1222±.1403	.1039±.0104

Difference......Medium N. – Low N. = .0307 ± .0113 (Dry Wt.). (Green Wt.) High N. – Low N. = .6853 ± .145.

	Sol. I (Low Nitrate), Roots		Sol. II (Medium Nitrate), Roots		Sol. III (High Nitrate), Roots	
	Green Wt.	Dry Wt.	Green Wt.	Dry Wt.	Green Wt.	Dry Wt.
Series 2, *20 days*	.7805	.0883	2.1530	.1853	2.0676	.1469
	.4583	.0667	1.4627	.1442	1.5892	.1213
	.7412	.0953	1.0294	.1088	1.4977	.1260
	.7340	.0900	.2330	.0396	.6623	.0568
	.5809	.0586	.3019	.0492	.7305	.0871
	.5020	.0734	.5391	.0680	1.3100	.1534
	.3729	.0549	1.2484	.1253	1.1824	.1124
	.4674	.0714	.5818	.0490	1.4398	.1102
Mean	.5799±.0367	.0747±.0036	.9437±.157	.0962±.0126	1.30996±.0346	.11426±.0074

Difference............(G. Wt.) High N. – Low N. = .7301 ± .0504. (Dry Wt.) High N. – Low N. = .0396 ± .0082.
(G. Wt.) High N. – Medium N. = .3663 ± .161.

importance upon composition of the nutrient solution. It would seem that when great emphasis is placed upon concentration as the cause in altering the ratio of tops to roots, as has been done by certain English workers in this field, greater care should be taken in checking up solutions used in order to make sure that there are sufficient mineral nutrients present at all times in the solution, for we cannot avoid the conclusion that one or more ions may become limiting factors in these more dilute solutions. Hoagland has shown that NO_3, PO_4, and K may be exhausted if the solution is run long enough without renewal. Starvation and concentration effects may be entirely different, yet their outward manifestation may often be indistinguishable.

The hydrogen-ion concentration was carefully checked for each set of experiments. The pH value ranged from 5.59 to 6.47. Though the low-nitrate solution had the highest hydrogen-ion concentration when it had also the highest total concentration (3,075 p.p.m.), this hydrogen-ion concentration could not be a factor in determining the ratio of tops to roots of plants growing in it, since the ratio is of the same relative order in respect to those of medium-nitrate and high-nitrate solutions as it was when the hydrogen-ion concentrations of the three solutions had the same value.

Proof is brought forth in the pure-culture experiments that nitrates have no direct checking effect upon roots, but that, on the other hand, the growth of roots is increased directly with the nitrate content of the solution, provided the disturbing influence of tops is not at hand. Thus, since there is no direct checking action of nitrates upon root growth, we shall have to explain the increased ratio of tops to roots on some other basis. Miss Brenchley (2) has offered an explanation of this phenomenon as follows:

> It seems as though the plant makes every endeavor to supply itself with adequate nutriment, as if, when the food supply is low, it strives to make as much root growth as possible so as to offer the greatest absorbing surface for whatever nutriment may be available.

Realizing that this explanation was not adequate, she has later offered a more elaborate explanation (3). Both explanations are purely teleological and do not give the plant physiologist any satisfaction as to the mechanism by which the tops in plants come to make such increase over roots.

Livingston's (17) explanation, which is based upon his experiments with plants growing in poor soil, is that the poor soil brings about such morphological changes in the root as to render it incapable of absorbing water, and thus, that the growth of tops is limited because of an inadequacy of water.

Curtis (36) has suggested that the effect of nutrients, especially of nitrates and phosphates, upon root growth might result, not from any direct action on or in the roots, but from an indirect effect caused by a change in the supply of food available for roots through the effect of the nutrient upon the use of the food by the tops.

In the experiments studied here, we find the increase of ratio of tops to roots to be due to nitrate ions. It has been shown, further, that nitrates do not retard the growth of roots directly, but that, on the other hand, the root increases in growth in the presence of nitrates if carbohydrates are also present. This fact shows that carbohydrates may be a limiting factor.

Further evidence along this line is shown in some unpublished data of Mr. W. C. Muenscher of the department of botany of Cornell University. Using averages of large numbers of water cultures (12 in one case, 25 in another), he found that the ratio of dry weight of tops to roots (barley) was always greater for plants grown in the shade than for those in the unobstructed sunlight. A brief summary of his data (in dry weights) is as follows:

	Sunshine	Shade	Time of Year
(1) Ratio, $\frac{\text{Tops}}{\text{Roots}}$	5.10	7.84	Jan. 19 to Feb. 24
(2) Ratio, $\frac{\text{Tops}}{\text{Roots}}$	4.26	5.96	Aug. 4 to Sept. 8.

This table shows also that the ratio of tops to roots was higher for plants grown in winter months than for those grown in the summer-fall season. Working as he was with a full nutrient solution, the production of carbohydrates seems to be the limiting factor, which accounts for the difference under the two conditions. Since the amount of carbohydrates produced in the shade or during the season of relatively less sunshine would be relatively less than that produced in greater light, the tops in the shade or in the reduced light of winter would use relatively more of that amount, thus leaving less for the roots.

Results from the pruning experiments of Chandler (6) may also have bearing on this point. He has shown that, while pruning is a dwarfing process, it checks root growth more than it does top growth. It is possible that, in removing a large leaf surface which is not compensated for by new growth, the carbohydrate production is cut down, and, as the increased vigor of the remaining shoots following pruning tends to use the carbohydrates manufactured, there is a smaller amount to be carried to the roots.

In the case of nitrates, it is likely that, when the concentration of nitrates is increased, relatively more of the manufactured carbohydrates tend to be consumed in the growth processes of the tops. Little is left for distribution to the roots. The roots, therefore, will not make the same relative growth as tops, and their growth may be severely checked in this way. This will explain also the sparse development of aërial roots in the high-nitrate cultures.

Plants like flax which show no increase in ratio of tops to roots as the nitrate content in the solution is increased may not be able to absorb nitrates beyond a certain amount or may not be able to utilize them beyond a certain amount, which is adequate in the low-nitrate solution; thus nitrates do not seem to become the limiting factor at the concentrations used.

Summary and Conclusions

1. Very few researches have been carried on to determine the factors which affect the ratio of top growth to root growth in plants. A solution of this problem is of interest both to the plant physiologist and to the practical plant grower.
2. The purpose of the present study is to determine more exactly how increasing the nitrate content of a nutrient solution that is otherwise adequate for plant growth will affect the actual top and root growth as well as the ratios of top to root growth; and further to suggest an explanation of the mechanism of the results obtained.
3. Definite effects of particular mineral nutrients, under controlled conditions, upon top-root ratios, have been given little attention, though work has been reported as to the effect of poor soil and of a decrease in concentration of the nutrient solution.
4. It has not been satisfactorily demonstrated that decreased concentration as such will decrease the ratio of tops to roots in plants; on the other hand, it has been demonstrated in the present set of experiments that decreased concentration is ineffective in contrast with nitrate ions.
5. A combination of nutrient salts is devised and used whereby nitrate ions may be increased or diminished widely without disturbing very much the other components of the solution.
6. In all cases, barley and corn show significant increases in ratio of tops to roots as nitrate concentration of the solution is increased. This effect of nitrates was shown to be independent of the total concentration of the solution, and independent of the hydrogen-ion concentration.
7. Flax grown for 41 days did not show an increase in ratio of tops to roots as nitrate content of the solution was increased, nor was there an increase with age after 21 days.
8. The efficiencies of the three solutions, as judged by total dry weights of tops and roots, were not greatly different.
9. Roots were grown in pure cultures with a supply of sugar. Some had plumules only removed; others had plumules and endosperms removed; in the third set, only the tips of the roots (2 cm. to 3 cm.) were employed. The results showed clearly that nitrates do not check, directly, root growth; but they increased the growth of roots in all cases.
10. The fact is brought out that neither dry weight nor length of root is a safe measure of growth in plants.
11. Evidence has been given in these experiments that roots grown in pure cultures, in absence of light, are able to utilize the nitrates and carbohydrates present in the solution for growth and respiratory processes.

12. Conclusion: The increased ratio of tops to roots which results from increasing the amount of nitrate in the solution may be explained on the basis of increased use of carbohydrates in the tops because the greater nitrogen supply makes for greater growth. This results in a decrease in the supply of carbohydrates for the roots, which may bring about an absolute or a relative reduction of root growth.

This study was carried out in the laboratory of plant physiology at Cornell University, and the writer is deeply indebted to Professor O. F. Curtis, who suggested the problem, for valuable and helpful criticisms in the course of the work. The writer also owes thanks to Professor H. H. Love of the plant-breeding department, who furnished the pure line of barley used, and to Professor C. H. Hutchinson of the same department for the pure line flax seeds.

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